THE TIME OF OVULATION IN CHIMPANZEES*

JAMES H. ELDER

Objectivity in sex research during the past fifteen years has been attained chiefly in animal laboratories. The difficulty of applying rigidly controlled scientific technics to the problems of human sex physiology has been a serious handicap and partly accounts for the fact that less is known about the sexual cycle in man than in some of the lower primates.

Prominent among the controversial problems in this field is the question of the time of ovulation. Although the hypothesis of periodic fertility and sterility in the primates is now widely accepted, especially among biologists, evidence of skepticism may be seen in the frequent communications to medical, scientific, and lay journals which attempt to contradict such views. Many of these reports are of case histories based upon testimony, and, as such, are scarcely acceptable as scientific evidence. Using strictly experimental technics, observations are now being made by Burr and his associates (Burr, Lane, and Nims, Burr and Musselman) which may indeed change the entire status of the problem within the near future.

It is significant that, in a recent examination and summary of the data on ovulation time in women, Hartman²⁴ presents, as an important part of the evidence for periodic fertility, the results of his observations on monkeys. Of all the evidence available to Hartman at the time, only a small portion was comparable in accuracy and completeness to the observations on monkeys. Because the sexual cycle of the monkey is identical or very similar to that of women in all essential characteristics, Hartman's data constitute some of the best evidence we have for the primates in general (Willson³⁴).

Most of the advantages in using monkeys for sex research purposes are to be found also in the use of chimpanzees. In addition, there are a few characteristics which make these apes particularly desirable as subjects for studies of ovulation time: (1) closer morphological and physiological affinities with man, (2) especially prominent variations in size and appearance of the ano-genital region

^{*} From the Yale Laboratories of Primate Biology. The writer gratefully acknowledges the aid of the Committee for Research in Problems of Sex, National Research Council.

during estrus, and (3) a menstrual cycle consistently several days longer than in man and monkey.

The present report will not deal at length with the controversial aspects of the problem, notwithstanding the temptation to cite some of the reports of case histories, clinical observations, and statistical and questionnaire studies which do not agree with our own findings. It is believed that the observations reported herein, while numerically small, are much more reliable than many of these miscellaneous reports. Following a brief description of material and methods used, the results will be considered in conjunction with some of the facts and prevailing theoretical opinions concerning reproductive physiology in other primates.

The subjects used in this investigation are members of the colony maintained by the Yale Laboratories of Primate Biology at Orange Park, Florida. All of them have been under constant observation for several years. Accurate daily records are kept of the sexual status of each individual,* and, in most cases, these include all of the postpubertal history. The fecundity of every subject except one (Mamo) has been confirmed by one or more pregnancies. It is not known, of course, whether all of them have been ovulating regularly, but for the period of observation the menstrual cycles were fairly regular. A female is not ordinarily used in determinations of the fertile period unless she is showing regular cycles and is in good health. Exceptions are described below. Three mature males, all with known reproductive histories, were used in the study. For observations on reproductive processes, the advantages of system-

^{*} Detailed description of methods used in obtaining sexual status records has been made elsewhere (Elder and Yerkes¹⁵). Since an important part of these observations is the recording of external changes in the genitalia, a brief comment is offered here concerning the probable relation of the tumescent phase and ovulation. The influence of the follicular hormone upon the sexual skin in monkeys has been shown by several investigators (Allen, 2, 3, 4; Parkes and Zuckerman 22). Zuckerman and Fulton⁴⁰ produced a slight response to injections of estrin in an immature female chimpanzee. Recently in these laboratories a marked response of the sexual skin in immature chimpanzees promptly appeared after injections of theelin (unpublished observations). Zuckerman and Parkes⁴¹ state that, in the baboon, collapse of the swelling is synchronized with the occurrence of ovulation. Detumescence following a period of maximum swelling seems to be a consequence of the rupture of a mature follicle and a diminished production of estrin, but the evidence does not show clearly the exact temporal relationship of the two events. It is obvious that, once this relationship is determined in several individuals, we may be able to date ovulation from the time of detumescence.

atized and accurate information concerning the life histories of our subjects cannot be overemphasized. Space limitation, however, makes it necessary to restrict this historical material to the foregoing general remarks.

Methods of determining time of ovulation. Of the various methods used in the determination of ovulation time, those depending upon the introspection, memory, and testimony of the subject are, fortunately perhaps, not available to the biologist using infrahuman primates. On the other hand, he is able to use certain objective procedures which, for reasons of inconvenience or social restriction, cannot be employed with human subjects. Hartman's technic of rectal palpation of the ovaries, although used to a limited extent by a few gynecologists (Dickinson^{13, 14}), has proved successful only with monkeys. The controlled mating procedure likewise may be used satisfactorily only in the animal laboratories. Several methods have been, or may be, used with monkeys and apes. These include the two just mentioned, (1) rectal palpation, (2) controlled mating, and also (3) direct examination of the ovaries or search for free eggs, (4) study of the epithelial changes of the vagina and uterus, (5) measurement of the amount of follicle-stimulating hormone in the blood or urine, and (6) measurement of electrical potential differences associated with the ovulatory process.

The size and strength of the great apes present serious practical difficulties in the use of any of these methods which require physical restraint. Anesthetization is possible but not advisable for frequent or routine use. Chiefly for this reason, Hartman's palpation method has not been used with chimpanzees. Another practical difficulty is that the size and distribution of the ano-genital swelling in many females prevent access to the ovaries during the follicular phase of the cycle. Tinklepaugh³³ found the vaginal smear technic useful in following the chimpanzee cycle, since it is possible to secure the animal's co-operation with a relatively short period of training. is difficult to judge the reliability of this method as an indicator of ovulation. Young³⁶ found that even in the guinea-pig it did not provide dependable criteria for heat and ovulation. Some investigators accept the method as an indicator of changes in the rodent cycle, but reject it for the more complex primate cycle. Its use with primates has been most successful in the hands of Papanicolaou,³¹ whose results have been corroborated generally by Davis and Hartman¹² for monkeys. The method is, however, as Davis and Hartman conclude, valuable chiefly in the differentiation of phases of the cycle rather than in exact determinations.

The controlled mating method, by which most of our results were obtained, appeared at the outset of this investigation to be most easily adaptable for chimpanzees. It was described previously (Elder and Yerkes¹⁵) as follows:

This method consists simply of permitting a single, effective, sexual contact for a limited period of time within the cycle and subsequently determining whether or not fertilization has occurred. Before the procedure begins to yield positive results, however, much preliminary work is necessary. A subject may be allowed to mate only once during a cycle which means that several weeks are required for each trial. As an aid at the outset to the selection of appropriate days for mating were the records of sexual behavior, from which it was possible to make a few general predictions. For example, there were several instances of failure to mate during early and late phases of the cycle and when mating did occur only at these times it was, without exception, infertile. It was with such information as this that the task of excluding the non-fertile days began. The procedure originally adopted began with a series of mating opportunities using a given female at a late, probably infertile period of the cycle, and gradually advancing (usually by 1 day) the date of mating in succeeding cycles. Thus, for example, a female was used on the twentyfifth day of a given cycle, the twenty-fourth day of the next, and so on until a fertile mating occurred. The chief reason for this particular approach was to avoid the contingency of too many contemporaneous pregnancies. Later it became desirable to conduct the mating observations on the most probably fertile dates of the cycle. (p. 133)

In this earlier paper on the sexual cycle of the chimpanzee certain general statements were made concerning ovulation time, and behavioral observations were presented which were believed to be closely correlated with ovulation. It is now possible to present a more complete and detailed study of the controlled mating results. Further comments on the value and limitations of the controlled mating method will be given in a later discussion.

Results. Table 1 shows 17 cases in which pregnancy followed mating on the days indicated by the male symbol, and 5 cases (Nos. 2, 7, 8, 18, and 19) in which fertilization was strongly indicated but not positively confirmed. The letter "M" is used to represent the period of menstruation, while "m" shows the duration of maximal genital swelling. Increases and decreases in the size of the external genital area are indicated by + and — signs, complete detumescence

or absence of swelling by the small dots. The first 14 cases are arranged approximately in the order of length of cycle, from the longest cycle to the shortest, for the purpose of showing the temporal relation between cycle length and time of the fertile period. The length of cycle characteristic of each individual is indicated by the crosses. These represent the median—in many cases both median and mode—of all normal cycles for the individual. In all but one case (Soda) the number of cycles from which the medians were determined range from 10 to 29, with 20 or more cycles recorded for eight of the subjects.

Selecting Case 3 (Josie) for the purpose of illustration, the record shows that menstruation was observed on one day only, January 24, 1935. For the following six days the external genitalia were in a resting phase of no swelling. The tumescent period began on the eighth day, and on the sixteenth the maximal size was reached. This condition continued for nine days or until the twenty-fourth day of the cycle. Mating with insemination occurred on the twenty-fourth day, or fourteen days before the next menstrual period was expected. Detumescence appeared on the twenty-fifth day and was complete by the thirtieth. A slight swelling was observed on the thirty-seventh day, but menstruation failed to appear as anticipated.

The cases in Table 1 in which more than one mating is shown were obtained during the course of observations on female receptivity (Yerkes and Elder³⁵). While they carry somewhat less definite implications than the cases of isolated matings, they all show that ovulation occurs within a limited period. Moreover, a characteristic of every case in the table is the record of insemination within a few days of the beginning of detumescence. We have hundreds of records of matings at all times in the cycle but not a single instance of conception when coitus did not occur within the last six days of maximal swelling. Since this is common to all cases it suggests improbability of fertilization from matings occurring prior to the sixteenth day. This hypothesis is substantiated by the records of sterile matings which are presented later.

A few of the cases in Table 1 require special comment and interpretation:

Case 1 (Cuba). The fact that the date of fertile coitus occurs late in this case, even though the preceding cycles are of average length, may be due to the effect of illness during the early part of the reproductive cycle. Records in the laboratory files indicate that a period of illness began on April 7th, two

TABLE 1

Isolated and controlled fertile matings and their relation to menstruation, maximal genital swelling, and cycle length in 13 chimpanzees

Case	Date of	Name of				Day	Days of cycle				
Мо.	Menstruation	Animal	12345	6 7 8 9	10 11 12 13 14 15	16 17 18	21 22 23 24 25	19 2021 22 23 24 25 26 27 28 29 30 31	31 32 33 34 35	32 33 34 35 36 37 38 39 40 41	41 42 43 44 45
-	APR. 9, 1937	CUBA (46)		•	+ + +	+ + + +	E. E. E.	- E E E	× ·	•	•
2	NOV. 10, 1933	MAY (32)	N N N N	•	•	E + +		! ! !		× + + +	+ + + +
10	JAN. 24, 1935	JOSIE (3C)	· · ·	+++••	* * * * *		- w w w w	1	•	· · ·	•
4	MAR. 10, 1937	MAY (32)	2 2	+++++	+ + + +		E	•	•	× · - + +	+ + +
က	JUNE 20, 1935	MONA(36)	MMM	+ + + +			w	•	* * * * * * * * * * * * * * * * * * *	+++	+ + + +
9	JULY 28, 1936	DI TA (40)	· N M W	+++••	E E + + +			• • • -	× ·	+ + + + •	
2	SEPT. 29, 1936	CUBA(46)	W	++++	E + + + +		· · E	+	+ × + + +		# + -
80	MAY 3, 1936	CUBA (46)	W W W	w++••		 	• • u	•	×	+	
o	NOV. 13, 1935	LIA (56)	M + + + +	-+-+-	+	m m	• • • •	• • • •	× ·	+ + +	+ + + + 1
0	JULY 23, 1936	LIA (56)	M M · · ·	+++++	+++++	- + + + -	• • • •	•	× ·	• • • •	•
=	JULY 18, 1936	PATI (42)	M	+ + + +	# + +	# H H	•	+ + •	+ + + + +	1	+ + + +
2	OCT. 2, 1936	F1F1 (38)	+ W W W	+ + + +	E E E	**************************************	•	•	+ + + × +	· + + + +	•

			E + E + · · · + · · · · · · · · · · · ·	E + E + · · · + · · · · · · · · · · · ·
--	--	--	---	---

+ = genital swellingdecreasing = insemination X = median length of all cycles - = no swelling, complete detumescence

m = maximum swelling M = menstruation

+ = genital swelling increasing

Pregnancy definitely confirmed in all cases except numbers 2,7,8, 18, and 19 B = abortion or bleeding of non-menstrual type

days before menstruation, and lasted for a week. The appearance of genital swelling was delayed several days, as comparison with other cases in the table reveals. This is a peculiarly important case in establishing the relationship between genital swelling, ovulation, and menstruation. It will be referred to later in a discussion of this topic.

Case 2 (May). Cycles of this animal show a median length of forty days with none shorter than thirty-six days. The cycle preceding the one represented was of forty-one days. Ovulation should occur, in cycles of this length, on the twenty-fifth or twenty-sixth day after the beginning of menstruation. Although placental tissue was not recovered it is believed that defective implantation and early abortion were responsible for amenorrhea of forty-five days which followed insemination on the twenty-fifth day.

Case 7 (Cuba). Eighteen days after this isolated mating bleeding appeared during maximal swelling, a coincidence which has never been observed except in association with early abortion.

Case 8 (Cuba). Pregnancy was suspected because her entire menstrual history presents no failure of menstruation to appear as expected except on two occasions when pregnancy was definitely confirmed.

Case 18 (Mamo). A case of the long cycle type. The cycle previous to the one represented was of forty-one days. Dates of mating are sixteen and fifteen days before expected menstruation, which failed to appear but was supplanted by genital swelling. Thirty-four days after mating profuse bleeding occurred (three weeks late) and continued in abundant flow for seven days. Except for the unusual hemorrhage no evidence of abortion was found, but the animal was caged at the time in a large outdoor enclosure where small quantities of embryonic tissue probably would have escaped notice. Following this prolonged bleeding another three weeks elapsed before signs of tumescence reappeared.

Case 19 (Mimi). Another example of the long cycle type. Cycles between forty and fifty days in length are common in this individual. The record is included chiefly because of the unprecedented occurrence of profuse bleeding for nine days following the period represented. The time of mating, in its relation to the time of maximal swelling and to the end of the cycle, conforms with the general tendency of the group.

Cases 20, 21, and 22 (Pati, Cuba, Soda). In these 3 cases male and female were caged together continuously, the copulative period being determined by examination of vaginal smears twice daily. The peak of receptive phase, as indicated by behavior, frequency of copulation, and spermatozoa count was reached on the sixteenth day with Pati and the nineteenth day with Soda. The copulative period in Case 20, the only one in the table in which the female was dominant over the male, probably coincides very closely with female receptivity. These 3 cases show the restriction of the fertile period to the mid-cycle range. Although opportunity for copulation was present at all times, it did not appear early or late in the cycle.

While positive results of isolated matings shown in Table 1 provide the clearest evidence of the fertile period in chimpanzees, it is also necessary to show that matings at other times in the cycle are sterile. Figures 1 and 2 give these results. Since rejections of the female by the male are related to periodicity of estrus and ovulation, the total number of mating opportunities are represented in the upper curve. The shaded areas of both figures show the number

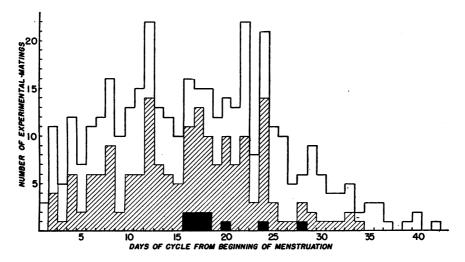


Fig. 1. Distribution of mating opportunities on days of the cycle counted from the beginning of menstruation. The top line shows the total number of opportunities. The cross-hatched portion of the figure represents the proportion of positive responses (copulation with insemination). Fertile matings are shown in black.

of experimental matings in which insemination occurred. Fertile matings (only 9 isolated and definitely confirmed cases are used) are shown in black. These results were compiled from the mating records of all the females (except Mamo) listed in Table 1 and three mature males. In order to keep the data of both figures comparable only the matings in regular cycles are used. The 381 mating opportunities shown in Figures 1 and 2 therefore represent a selected sampling from a total of more than 500.

In Figure 1 there are 80 matings with insemination during the first fifteen days of the cycle, none of which was fertile. Most of the fertile matings shown fall on the sixteenth to twentieth days,

with one as late as the twenty-eighth day. This rather wide range of thirteen days is attributed to variations in cycle length, appearing either as a consistent individual characteristic or as occasional deviations from individual norms. Figure 2 shows the data of Figure 1 as it appears when the day of each mating is counted from the end of the menstrual cycle instead of the beginning. Here there is somewhat greater uniformity in the ratio of positive responses (mat-

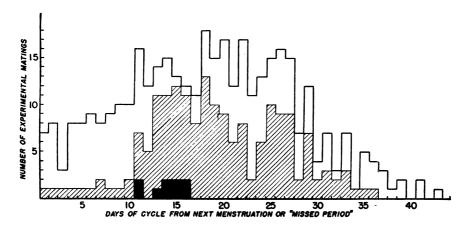


Fig. 2. Distribution of mating opportunities dated from the first day of the following menstruation, showing the proportion of positive responses (cross-hatched area) and fertile matings (black).

ing with insemination) and total mating opportunities. During the last ten days of the cycle (the first ten days in the figure) there are few positive responses, but on the fifteenth day 11 out of 12 mating opportunities were positive and 2 of these were fertile. One individual is responsible for all but 2 of the positive responses between days 1 to 10 as well as 19 of the 45 on days 24 to 30. Figure 2 reduces the range of fertile matings from thirteen days to six. Since there is normally no menstruation to count backward from, following a fertile mating, all the cycles for a given animal are used to determine the median time elapsing between the first day of detumescence and the next menstrual period. In 8 subjects out of 12 this time is ten or eleven days. Then, to fix the date of a fertile mating in reference to the predicted but unknown

end of the cycle, the number of days by which the date of mating precedes the detumescent phase is added to the latter. If, for example, Dita's cycle terminates eleven days (median of 20 cycles) after the first day of detumescence and a fertile mating occurs five

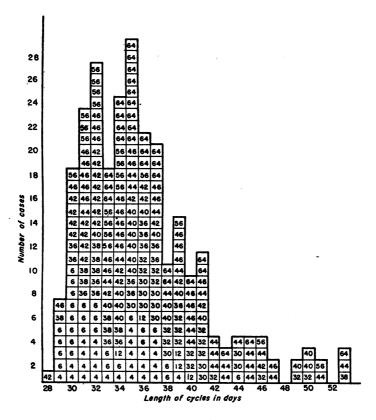


Fig. 3. Frequency distribution of the lengths of 263 sexual cycles. Numbers within each square refer to individual animals as listed in table 1.

days before detumescence appears, it is sixteen days before the first menstrual day is anticipated.

Figure 3 shows the length and distribution of cycles for all subjects. A similar chart was shown in an earlier report (Elder and Yerkes¹⁵) but the present one incorporates 99 additional cycles, including those for Mimi which were not shown previously. The

small numbers within each square in Figure 3 identify individual animals in conformity with official laboratory designations.

Ovulation time in other primates. There are no observations on ovulation time in chimpanzees with which the foregoing results may be compared, but they may be considered in relation to some of the more objectively determined data on other primates. The Rhesus macaque, with a typical menstrual cycle of twenty-eight days in length, ovulates on the tenth to fourteenth day, according to Corner^{10, 11} and Allen.^{1, 2} In the baboon it occurs near the middle of the cycle (Zuckerman^{38, 39}; Zuckerman and Parkes⁴¹). According to Zuckerman, 39 the menstrual cycle of the baboon averages 31.4 days in length. Gillman, 17 using the vaginal smear technic of Papanicolaou, 31 found the copulative phase of the cycle in the Chacma baboon ranging from the eleventh to twenty-sixth days. He gives the time of ovulation as days 18 to 20, but also states that the length of cycle for his subjects ranged from thirty-five to forty-two days. Hartman^{21, 22, 23, 24} found that ovulation in monkeys occurred most frequently on the thirteenth day following the first day of the preceding menses. In 108 cycles approximately two-thirds of the ovulation dates fell on days 11 to 14.24 No instance of ovulation in the monkey has been observed earlier than the eighth day nor later than the twenty-third day of the cycle. Only 5 cases were later than the sixteenth day. These observations were made on animals with cycles ranging in length from about fourteen days to over fifty days.

It has already been noted that the date of fertile coitus in chimpanzees falls relatively early in short cycles and late in long cycles; and, in order to avoid the necessity of qualifying statements for each individual with cycles widely differing from the mean, the time elapsing between coitus and the following anticipated menstruation is given. If we think only in terms of averages or modes, we see that the monkey ovulates, in a typical cycle of twenty-eight days, about fifteen days before the beginning of menstruation. It would appear, then, notwithstanding the differences in length of the menstrual cycle in monkey and chimpanzee, that both are alike in respect to the time of ovulation.

This conclusion seems rather incongruous, however, if the data for monkeys are examined more closely. Thus Hartman²⁸ found that the post-ovulatory period of the cycle in monkeys was quite variable and was chiefly responsible for the differences in total cycle length; whereas in chimpanzees the pre-ovulatory period—or rather the

period before detumescence—is the more variable (Elder and Yerkes¹⁵). Notwithstanding the possibility that this may be a fundamental physiological difference, central tendencies indicate that the difference in time of ovulation corresponds closely to the difference in length of the menstrual cycle. Since about 3 per cent of chimpanzee cycles are as short as twenty-eight and twenty-nine days, presumably a large sample would show a few cases of ovulation as early as the fourteenth day. Similarly, because of a small percentage of monkey cycles which approach the maximum length of the chimpanzee cycle, we should find an occasional late date of ovulation in the monkey. Apparently this is exactly what has happened. As additional data have accumulated for the Carnegie monkey colony under Hartman's observation, he has found the range of ovulation days extended until it now includes one case each on days 17, 18, 20, 21, and 23.

When we attempt to compare the time of ovulation in chimpanzee and man we are confronted with a considerable amount of conflicting evidence, somewhat inconclusive in its indications as to when the human female ovulates. There is, however, general agreement that it does not occur during the first few days of the average menstrual cycle and probably not during the last ten days The sharpest divergence of opinion is on the question of ovulation during the pre-menstrual period, one group contending that it occasionally occurs during this period, another insisting that it never does. The recent increase in clinical and experimental data may be expected eventually to settle the issue. Most of the calendar systems and safe-period charts prepared for women are based on the Ogino-Knaus assumption that ovulation does not occur during the pre-menstrual period of ten days no matter what the length of cycle may be. It hardly can be denied that the intelligent application of this method is generally effective as a contraceptive technic. The growing mass of records of successful use of the method greatly exceeds the reports of failure (Latz, 26 Miller, 29 Latz and Reiner 27, 28).

Fortunately, for the purpose of our comparison, the many thousands of records for women include a few cases in which the menstrual cycle exceeds forty days in length. These usually constitute from 3 to 5 per cent of the total. In these long cycles the theoretical prediction that ovulation occurs after the twentieth day seems to be verified in practice. If a group of women whose menstrual cycles varied between thirty-four and forty days were selected for study, the writer believes that determinations of ovulation time would cor-

respond to the findings reported here for chimpanzees. pletely objective studies like those of Allen, Pratt, Newell, and Bland, 5, 6 in which free eggs are washed from the Fallopian tubes, it should be expected that most of the eggs would be found about the fourteenth day of the cycle, since most of the observations are from women with cycles of average length. Only in four or five cases out of a hundred should we expect to find eggs later than the twentieth day, unless it were possible to select patients with long menstrual cycles. It is just as important, of course, to study the short cycles if we wish to get a complete picture of the ovulation-menstruation relationship. It is impossible to do this with chimpanzees because they never have cycles shorter than twenty-eight days. This seems to explain why no fertile mating has occurred before the sixteenth It was suggested above that this limit undoubtedly will be lowered slightly as more cases are added, but since the present minimum cycle length of twenty-eight days seems to be a stable limit, we hardly expect to find, in our present colony of chimpanzees, a case of ovulation earlier than the thirteenth day. Such an occurrence would demand a restatement or revision of present concepts.

Discussion. No small amount of confusion has arisen from the failure to take cycle length into account when predicting the date of ovulation. It is for this reason that pleas have often been made to women for more accurate and complete records of their menstrual cycles. Even some of the best reports of clinical data have failed to give the essential facts relating to previous menstrual histories of patients from which the data were obtained. How shall we interpret variations in ovulation time from the seventh to the twenty-fifth days unless we assume that cycle length is the chief determiner?

It seems probable that discrepancies between intra- and interspecies comparisons will continue to present a confusing picture until we conceive of a fairly constant and well-regulated endocrine control of menstruation which is determined or set going by ovulation (Ogino, ³⁰ Knaus²⁵). Whatever its nature may be—perhaps a growth or degeneration process of the corpus luteum—the time factor seems to be important.

Engle, Smith, and Shelesnyak¹⁶ report results of studies on the rôle of estrin and progestin in experimental menstruation which strongly support this view. They found that menstruation in monkeys occurred in the presence of a high level of estrin in the blood, which suggested that the Allen-Corner estrin prive hypothesis was not entirely adequate to account for menstruation. They also

showed that administration of the corpus luteum hormone, progestin, prevented bleeding for the duration of treatment. They conclude that menstruation results from a cessation in the secretion of the corpus luteum. It is not difficult to see from this evidence how the functional period of the corpus luteum in the non-gravid animal may be responsible for a constant temporal relationship between ovulation and menstruation.

The importance of this relationship is beginning to be realized, but it is still ignored or under-emphasized in some of the literature. If it were desired to avoid conception in chimpanzees, a disregard of this principle would lead to some failures, just as it occasionally does among women who believe they should ovulate at the middle of their menstrual cycle. Case 3 in Table I represents just such an This was one of the first experimental matings to be "accident." The long menstrual cycles of this animal were not taken into account and she was mated at what was believed to be a sterile period. Case 1 illustrates this point, but it also shows that counting backward from the anticipated time of bleeding may not always lead to an accurate prediction if there is a delay or irregularity in the ovarian cycle. Definite knowledge of exposure, shock, or illness may enable one to predict a prolonged cycle, but in women the accuracy of the prediction cannot be checked until the cycle has ended; in a chimpanzee an approximate check is provided by the time of genital swelling and detumescence. Because of the uncertainty as to how long ovulation may be delayed, it appears that the early part of the cycle is "safer" than the pre-menstrual period, except—it must be added—in those individuals who have experienced extreme irregularities from very short to long cycles.

The use of the isolated mating technic is advantageous, particularly in preliminary studies, but it cannot be said to yield more than close approximations. It is difficult, for example, to demonstrate that ovulation has not occurred in a given cycle, and in interpreting the results of the method it is necessary to make certain assumptions concerning the life span of sperm and ova. Hartman,²⁰ Hammond and Marshall,¹⁹ and others have shown that this time is brief for the mammalian ovum—certainly not more than twenty-four to forty-eight hours and much shorter than this in some species (Young and Blandau³⁷). Similar evidence, notably the experiments of Hammond and Asdell,¹⁸ shows that sperm in the rabbit rapidly lose their fertilizing power after ten hours in the genital tract. The writer has repeatedly examined vaginal smears taken from chimpanzees at suc-

cessive intervals after mating. Motile sperm have never been seen later than three hours after insemination. Usually they die within an hour. The period of survival probably is somewhat longer in the uterus. It is hoped that some of these questions may be answered more directly by an investigation now in progress which is attempting exact determinations of ovulation time by means of the vacuum tube microvoltmeter developed by Burr, Lane, and Nims⁸ and used successfully by Burr, Hill, and Allen⁷ in recording the process of ovulation in the rabbit. Measurements are taken daily throughout the cycle, with special attention being given to that period which the present results indicate as fertile. The number of observations already made is small and cannot support a general statement of results, but the present indications suggest a confirmation of the controlled mating data (Finch, Yerkes, and Elder^{16a}).

Summary. Observations on 13 chimpanzees show a period of fertility ranging from the sixteenth to the twenty-eighth day of the menstrual cycle. Isolated matings, after which pregnancy was definitely established, were made on the following days: 2 each on the sixteenth, seventeenth, and eighteenth, and 1 each on the twentieth, twenty-fourth, and twenty-eighth days. Eleven other cases are shown in which the fertile period was limited to a narrow range.

Results strongly indicate that the typical length of the menstrual cycle is of great importance in determining the time of ovulation in a given individual. If this date is counted from the end of the cycle instead of the beginning the effect of differences in cycle length are minimized. This also permits more direct comparisons with other primates. Assuming the life span of sperm and ova to be not more than forty-eight hours, ovulation in chimpanzees occurs about four-teen days before the beginning of the next menstrual cycle. This is in close agreement with some of the evidence for man and monkey.

REFERENCES

- 1 Allen, Edgar: The time of ovulation in the menstrual cycle of the monkey, *Macacus rhesus*. Proc. Soc. Exper. Biol. & Med., 1926, 23, 381-83.
- 2 Allen, Edgar: The menstrual cycle of the monkey, Macacus rhesus: Observations on normal animals, the effects of removal of the ovaries and the effects of injections of ovarian and placental extracts into the spayed animals. Contr. Embryol., Carnegie Institution of Washington, Publ. No. 380, 1927, 19, 1-44.
- 3 Allen, Edgar: Reactions of immature monkeys (Macacus rhesus) to injections of ovarian hormone. J. Morphol., 1928, 46, 479-519.

- Allen, Edgar: Further experiments with an ovarian hormone in the ovariectomized adult monkey, Macacus rhesus, especially the degenerative phase of the experimental menstrual cycle. Am. J. Anat., 1928, 42, 467-87.
- Allen, E., Pratt, J. P., Newell, Q. U., and Bland, L. J.: Recovery of human ova from the uterine tubes. Time of ovulation in the menstrual cycle. J. Am. Med. Asso., 1928, 91, 1018-20.
- Allen, E., Pratt, J. P., Newell, Q. U., and Bland, L. J.: Human tubal ova; related early corpora lutea and uterine tubes. Contr. Embryol., Carnegie Institution of Washington, Publ. No. 414, 1930, 22, 45-76.
- Burr, H. S., Hill, R. T., and Allen, E.: Detection of ovulation in the intact rabbit. Proc. Soc. Exper. Biol. & Med., 1935, 33, 109-11.
- Burr, H. S., Lane, C. T., and Nims, L. F.: A vacuum-tube microvoltmeter for the measurement of bioelectric phenomena. Yale J. Biol. & Med., 1936, 9, 65-76.
- 9 Burr, H. S., and Musselman, L. K.: Bio-electric phenomena associated with menstruation. Yale J. Biol. & Med., 1936, 9, 155-58.
- Corner, G. W.: Ovulation and menstruation in Macacus rhesus. Contr. Embryol., Carnegie Institution of Washington, Publ. No. 332, 1923, 15, 73-101.
- Corner, G. W.: Relation between menstruation and ovulation in the monkey; 11 its possible significance for man. J. Am. Med. Asso., 1927, 89, 1838-40.
- 12 Davis, M. E., and Hartman, C. G.: Changes in vaginal epithelium during pregnancy in relation to the vaginal cycle. J. Am. Med. Asso., 1935, 104, 279-85.
- Dickinson, R. L.: Ovulation in women studied by bimanual palpation. Am. J. Obst. & Gynec., 1936, 32, 828-31.
- 14 Dickinson, R. L.: The technic of timing human ovulation by palpable changes in ovary, tube and uterus. Am. J. Obst. & Gynec., 1937, 33, 1027-33.
- 15 Elder, J. H., and Yerkes, R. M.: The sexual cycle of the chimpanzee. Anat. Rec., 1936, 67, 119-43.
- 16 Engle, E. T., Smith, P. E., and Shelesnyak, M. C.: The rôle of estrin and progestin in experimental menstruation, with especial reference to the complete ovulatory cycle in monkeys and human beings. Am. J. Obst. & Gynec., 1935, 29, 787-97.
- 16a Finch, G., Yerkes, R. M., and Elder, J. H.: Bodily electrical potential changes associated with ovulation and early pregnancy in the chimpanzee. Proc. Soc. Exper. Biol. & Med., 1937, 37, 560-63.
- 17 Gillman, J.: The cyclical changes in the vaginal smear in the baboon and its relationship in the perineal swelling. S. African J. Med. Sci., 1937, 2, 44-56.
- 18 Hammond, J., and Asdell, S. A.: The vitality of the spermatozoa in the male
- and female reproductive tracts. Brit. J. Exper. Biol., 1926, 4, 155-85. Hammond, J., and Marshall, F. H. A.: Reproduction in the rabbit. Edin-19 burgh and London, Oliver and Boyd, 1925.
- 20 Hartman, C. G.: Observations on the viability of the mammalian ovum. Am. J. Obst. & Gynec., 1924, 7, 40-43.
- 21 Hartman, C. G.: Uterine bleeding as an early sign of pregnancy in the monkey (Macacus rhesus), together with observations on the fertile period of the menstrual cycle. Johns Hopkins Hosp. Bull., 1929, 44, 155-64.

- 22 Hartman, C. G.: Studies in the reproduction of the monkey Macacus (pithecus) rhesus, with special reference to menstruation and pregnancy. Contr. Embryol., Carnegie Institution of Washington, Publ. No. 134, 1932, 23, 1-161.
- 23 Hartman, C. G.: Pelvic (rectal) palpation of the female monkey, with special reference to the ascertainment of ovulation time. Am. J. Obst. & Gynec., 1933, 26, 600-08.
- 24 Hartman, C. G.: Time of ovulation in women: a study of the fertile period in the menstrual cycle. Baltimore, Williams and Wilkins, x + 226 pp., 1936.
- 25 Knaus, H.: Periodic fertility and sterility in women: a natural method of birth control. Vienna, Wilhelm Maudrich, 162 pp., 1934.
- 26 Latz, L. J.: The rhythm of sterility and fertility in women. Chicago, Latz Foundation, viii + 136 pp., 1934.
- 27 Latz, L. J., and Reiner, E.: Natural conception control. J. Am. Med. Asso., 1935, 105, 1241-46.
- 28 Latz, L. J., and Reiner, E.: Failures in natural conception control and their causes. Illinois Med. J., 1937, 71, 210-16.
- 29 Miller, A. G.: Progress in the study of physiologic sterility. Clin. Med. & Surg., 1935, 42, 19.
- 30 Ogino, K.: Conception period of women. Harrisburg, Pa., Med. Arts Pub. Co., 95 pp., 1934.
- 31 Papanicolaou, G. N.: The sexual cycle in the human female as revealed by vaginal smears. Am. J. Anat., 1933, 52, 519-637.
- 32 Parkes, A. S., and Zuckerman, S.: The menstrual cycle of the primates. II. Some effects of cestrin on baboons and macaques. J. Anat., 1931, 65, 273-76.
- 33 Tinklepaugh, O. L.: Sex cycles and other cyclic phenomena in a chimpanzee during adolescence, maturity, and pregnancy. J. Morphol., 1933, 54, 521-47.
- 34 Willson, Prentiss: Present knowledge on the rhythm of human fertility. Some biological and physiological considerations affecting its practical application to problems of sterility and birth control. Med. Annals, Dis. of Col., 1937, 6, 87-99.
- 35 Yerkes, R. M., and Elder, J. H.: Oestrus, receptivity, and mating in chimpanzee. Comp. Psychol. Monog., 1936, 13, 1-39.
- 36 Young, W. C.: The vaginal smear picture, sexual receptivity and the time of ovulation in the guinea-pig. Anat. Rec., 1937, 67, 305-25.
- 37 Young, W. C., and Blandau, R. J.: Ovum age and the course of gestation in the guinea-pig. Science, 1936, 84, 270-71.
- 38 Zuckerman, S.: The menstrual cycle of the primates. I. General nature and homology. Proc. Zool. Soc., Lond., 1930, 691-754.
- 39 Zuckerman, S.: The social life of monkeys and apes. New York, Harcourt, Brace, xii + 356 pp., 1932.
- 40 Zuckerman, S., and Fulton, J. F.: The menstrual cycle of the primates. VII. The sexual skin of the chimpanzee. J. Anat., 1934, 69, 38-46.
- 41 Zuckerman, S., and Parkes, A. S.: The menstrual cycle of the primates. V. The cycle of the baboon. Proc. Zool. Soc., Lond., 1932, 139-91.